

BIOLOGY AND LIFE HISTORY OF THE NUDIBRANCH MOLLUSC, *CORYPHELLA STIMPSONI* (VERRILL 1879)

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Verrill (1879) originally described *Coryphella stimpsoni* from Eastport, Maine and in 1880 reported its range from Massachusetts Bay to Halifax, Nova Scotia. Bergh (1885) recorded the morphology of *C. stimpsoni* based on a preserved specimen collected in Nova Scotia and sent to him by Verrill. Krause (1892) and Knipowitsch (1902) found *C. stimpsoni* in Northern Europe and the latter described a new variety based on radular variation.

In October, 1968 and 1969 a large number of *Coryphella stimpsoni* were encountered moving over mud flats in what appeared to be a mass migration at the Moosehorn Wildlife Refuge, Edmunds, Maine. The nudibranchs were taken to the Northeastern University Marine Science Institute where further observations were made which are reported here.

MATERIALS AND METHODS

Observations and measurements were made on living animals whenever possible. Radular mounts were prepared utilizing Turtox CMCS and Gomori trichrome stain; the latter one clearly differentiated the teeth from the radular membranes.

At the Marine Science Institute, the specimens were maintained in plexiglass tanks. Egg masses were isolated in glass dishes on the water table. Newly hatched specimens were relaxed in 5% $MgCl_2$, fixed in Hollande's fluid, sectioned and stained. Adult specimens were relaxed in 8% $MgCl_2$, fixed in Hollande's fluid and 10% formalin. Representative specimens have been deposited at the U. S. National Museum (Smithsonian) and in the Mollusk Department of the Museum of Comparative Zoology at Harvard University.

RESULTS

Description of the adults

Living specimens ranged from 13-20 mm in length and the foot measured 4.5-5 mm in greatest width. The cerata are evenly distributed in two longitudinal bands on the dorsal surface and extend anteriorly beyond the position of the paired rhinophores. The cerata are largest medially and decrease in size while increasing in number toward the lateral margin of the mantle (Fig. 1).

The head is large and forms a characteristic trefoil due to the presence of large rounded lateral lobes. The color of the head and tentacles is an opaque white, identical to the body color. The smooth oral tentacles are slightly longer, taper more abruptly, are wider at the base and narrower at the tip than the rhinophores. During movement, the tentacles are continually brought in contact with the sub-

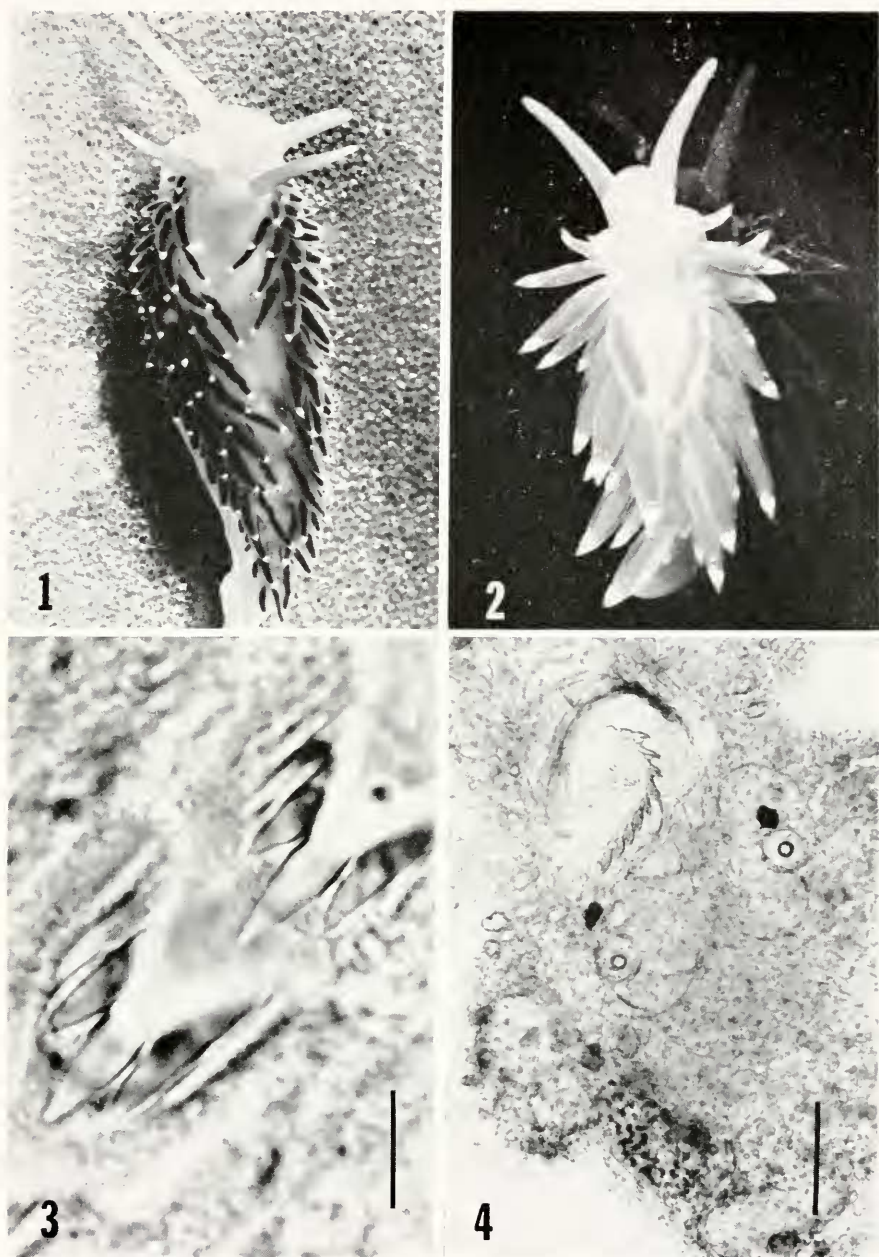


FIGURE 1. Adult *Coryphella stimpsoni* measuring 33 mm in length.

FIGURE 2. Juvenile *C. stimpsoni* measuring 6 mm in length.

FIGURE 3. Radula of a juvenile *C. stimpsoni* at 7 rachidian tooth stage. Scale equals 0.01 mm.

FIGURE 4. Juvenile at 8 rachidian tooth stage showing radula, eyes, cerebral ganglion and statocysts. Scale equals 0.03 mm.

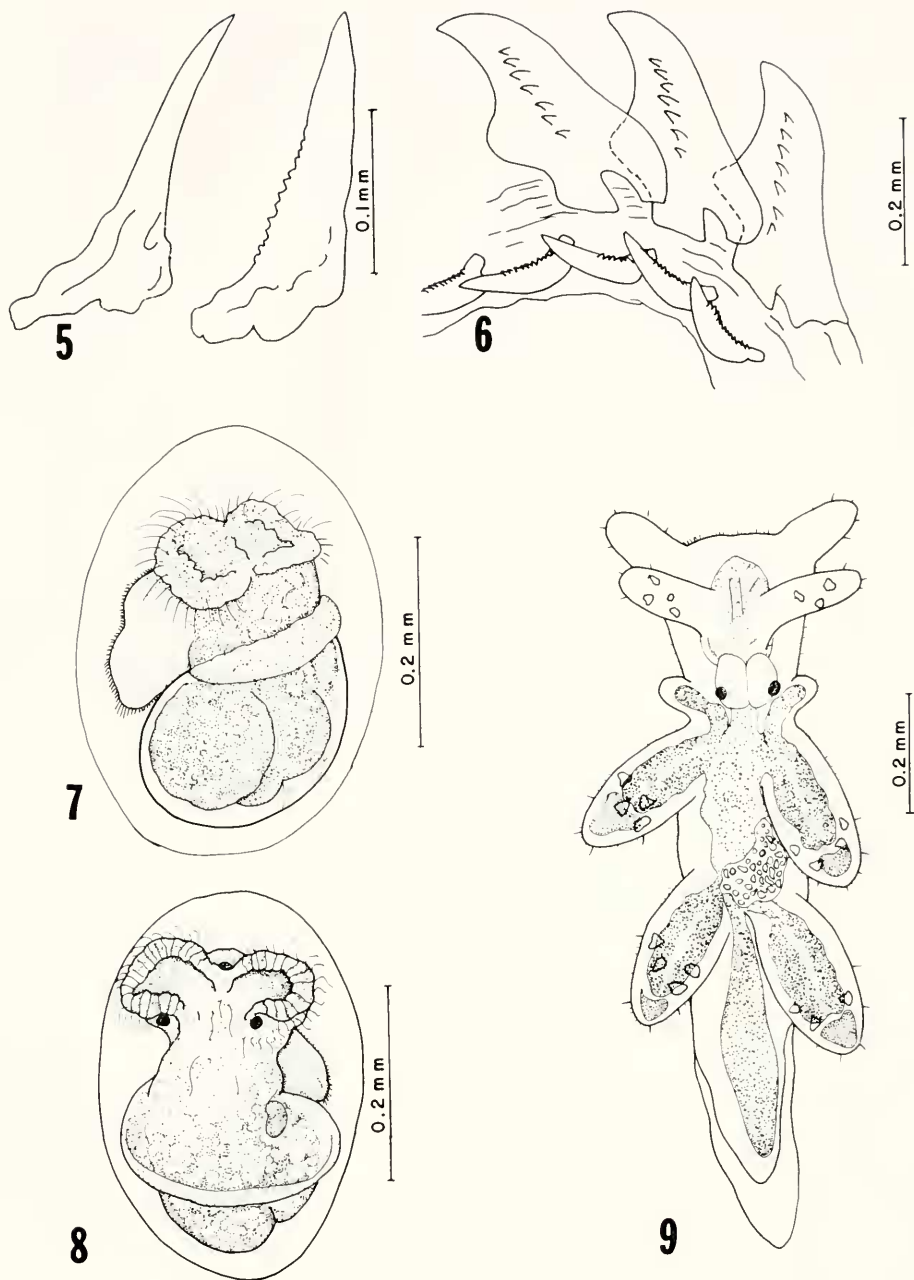


FIGURE 5. Two lateral radular teeth of an adult *C. stimpsoni* showing variations of the shape and presence of denticles.

FIGURE 6. Portion of radular ribbon of *C. stimpsoni* showing the single row of rachidian teeth and laterals of one side.

strate in a probing manner and are utilized for holding the prey during feeding. The rhinophores are very contractile and can retract to one half their length upon being touched or when they come in contact with a foreign object such as a sea anemone. When contracted the rhinophores appear to be ringed but in extension during undisturbed activity this configuration is lacking. In the living forms the rhinophores are tinged a light orange and the distal third has a white external pigmentation.

The foot is broad, well developed with two short anterior lateral extensions which add $\frac{1}{3}$ to the total width of the foot at their point of origin. The width of the foot is relatively constant and the posterior end forms a rather abrupt point. During crawling activities the posterior portion of the foot does not project far from the body.

The cerata have a central core of the digestive gland which is red-brown in color. In each ceras this core terminates at the distal end just before an epidermal pigmentation of white dots appears. In some cerata these external dots are numerous and close together forming a ring and the tip beyond this ring is the translucent white color of the body. The cerata are round in cross section and taper evenly toward the distal end. In several specimens there were patches of two to five cerata which did not contain the central core of the digestive gland.

The reproductive opening, anus and excretory pore all open on the right side of the animal between the mantle edge and the foot. The anus is located $\frac{3}{4}$ posteriorly on the right side, the genital complex anteriorly on the same side and the smaller excretory pore in between nearer the genital openings. The area between foot margin and the first longitudinal row of cerata is pigmented with an epidermal white pigmentation of the same type found associated with the cerata and the rhinophores.

The triserial radula is variable. In the fifteen radulae examined, the number of rows of teeth varied from 24–31. The denticulations on either side of the central tooth ranged from 8–13 and those of the lateral teeth varied from 9–11 fine denticles to no observable denticulations. On several radulae the younger lateral teeth of the ribbon appeared to be more slender and to have fewer denticles (Fig. 5).

The central rachidian teeth measured 0.28–0.38 mm in height (Fig. 6). The teeth are attached to the radular membrane by two square lateral projections which were described and figured by Krause (1892) and Knipowitsch (1902). The lateral teeth ranged between 0.17–0.22 mm in length and both slender and stout teeth as figured by Krause and Knipowitsch were found.

Two well-developed jaws are associated with the buccal mass. The masticating edges of the jaws form an oval ring lining the oral opening into the buccal mass. Bergh (1885) illustrated a portion of the masticating edge of the jaw showing the denticles which agrees with my observations. Under oil immersion the denticles are found to be covered with tubercles which are most prominent on the reflected

FIGURE 7. Side view of developing veliger of *C. stimpsoni* showing the mantle fold and shell.

FIGURE 8. Encapsulated veliger of *C. stimpsoni* with velum, foot, eyes, mantle fold and larval heart.

FIGURE 9. Juvenile *C. stimpsoni* with four primary cerata with differentiated cnidosacs. Note the beginning of the first pair of cerata in front of the anterior pair.

outer edges of the masticating portion and considerably worn down toward the oral opening into the buccal mass.

Feeding activity

When numbers of *C. stimpsoni* were observed in Maine, the animals were found crawling on an extensive mud flat. Screening of the substrate was undertaken to determine a possible food source for the nudibranchs. The burrowing anemones, *Edwardsia elegans* Verrill and *Halcampa duodecimcirrata* (Sars), were found in the same habitat and later in the laboratory when with these organisms, *C. stimpsoni* exhibited a definite feeding response. The feeding animal projected the outer lip and mouth forward and lowered the oral tentacles to hold the prey. The epidermis of the anemone was rasped away by the radula and ingested. Specimens collected in 1969 were maintained in the laboratory using the hydroid *Tubularia* sp. as their food organism.

Reproduction and development

Reproduction and development in *Coryphella stimpsoni* has been observed over a two-year period, and in each year the nudibranchs were collected in October, taken to the Marine Science Institute and held in the laboratory tanks. The animals copulated for several hours during which time the exchange of sperm occurred when the two individuals were aligned in opposite directions with their reproductive openings in communication. There was little movement during copulation.

Egg masses, when viewed from above, were normally deposited in concentric whorls starting from the center and moving counterclockwise. The coil thus produced varied from $1\frac{1}{2}$ – $2\frac{1}{4}$ whorls and adhered tightly to the surface on which it was extruded. In one case the individual whorl measured 2 mm in width and the entire egg mass measured 10 mm in diameter. The individual uncleaved eggs measured 0.25 mm in diameter and the egg capsule surrounding the single egg measured 0.41 mm in length by 0.30 mm in width. The egg masses were deposited over a period of approximately 15–20 days during the month of December. The algal species *Ascophyllum nodosum* and *Chondrus crispus* were introduced to the tanks and utilized by the nudibranchs for egg deposition. Although both these species are present on the intertidal area where the nudibranchs were collected and may serve as a substrate for egg deposition, *C. stimpsoni* also deposited eggs on the sides of the tanks and the underside of several rocks in the tanks.

Development time varied during the two years of observations and is influenced by temperature. The time of development from egg deposition until the juvenile crawled from the egg mass was 52 days at a temperature ranging from 4.0° C to 5.0° C. The time of development at a temperature ranging from 5.0° C to 8.5° C was from 25 to 34 days. This makes it difficult to predict development in nature and continual observations of development in the Maine habitat have not been made.

The eggs cleave equally to the four-cell stage and a quartet of micromeres are given off clockwise at the eight-cell stage. A rounded ball of small cells results from repeated cleavages. Soon after this a cap-shaped gastrula is formed with a

ventral depression. The gastrula changes shape to a rounded form and the velum begins to differentiate. There is no observable internal differentiation, the embryo appears opaque due to the presence of a large amount of yolk and there is no movement within the egg capsule.

Differentiation of the foot and velum of the nudibranchs continues with the development of two velar lobes and cilia. The foot, without an operculum, enlarges on the ventral side. At this stage a large yolk mass of the body begins to differentiate into three lobes. These lobes are partially united anteriorly, but posteriorly the mass on the left side is single and there are two smaller lobes on the right side. The two right lobes are united to one another and then together with the larger left yolk mass. The larvae begin to show some movement within the egg capsules. Further differentiation occurs with the formation of the mantle fold, the secretion of a thin shell surrounding the body of the veliger, and the development of a pair of eyes and statocysts. The veligers move within the egg capsule but not at any great speed and in many cases, they remain still with the velar cilia continuing to move randomly. The shell is very thin and is present for only a short period of time (Figs. 7 and 8).

While still in the capsule larval characteristics begin to disappear and the veliger begins to resemble an adult. The mantle fold moves posteriorly forming the edge of the mantle. The four primordia of the cerata develop in front of the fold which subsequently becomes indistinct. However, it can still be seen just above the large digestive gland and posterior to the cerata primordia. The velum is reabsorbed and the velar cilia are reduced to patches near the eyes. As the velum is reabsorbed the cilia on the muscular foot become active. Although the entire surface of the foot is covered, the cilia are numerous and close together along the anterior margin. These cilia cause the rotation of the embryo which is very minor at this stage. Small rudiments of the oral tentacles and rhinophores appear on the head and the dorsal portion of the visceral mass shows differentiation of four digestive gland primordia which develop simultaneously, in most cases while the nudibranchs are still within the egg capsule.

The juveniles hatch from the egg mass from 25 to 52 days after egg deposition depending on the temperature of the surrounding water during development. Several days before hatching, the interior portion of the stroma surrounding the eggs becomes opaque and is invaded by microorganisms. Nematodes, protozoans and harpacticoid copepods can be seen moving through the coils. The outside of the egg string remains intact for about a week after the hatching process is complete. The individual egg capsules become slightly opaque just prior to their rupture and when the capsule wall collapses the animal crawls away from the flaccid structure. Eclosion is not clear. There is a great deal of activity of the foot prior to hatching and the cilia of the foot, especially the numerous anterior cilia, beat continually. Juveniles which escape from the egg capsule have been found, in some cases, to have from two to four radular teeth present which they may use to rasp through the capsule.

Juveniles crawl directly from the egg capsule and take up an immediate benthic existence. They were positively phototactic and gathered on the sides of the vessels nearest the window if food was not present. However, if food was present, they crawled toward the hydroid to feed. The newly hatched juveniles appear

opaque white with large granules of yolk in the body. The body is well differentiated from the foot. The surface epithelium is entirely ciliated with greater concentrations of cilia on the anterior portion of the foot and around the mouth area. Stiff sensory bristles occur on the oral tentacles, rhinophore primordia and the four primary cerata. Statocysts and eyes are present and the small juveniles continue to move over the surface of the substrate by both muscular action of the foot and by ciliation of the foot. In an experimental group, mixed cultures of the algae *Dunaliella* sp., *Monochrysis lutheri* and *Isochrysis galbana* were introduced into the bowls. The algae could be seen rotating in the stomach and gave the digestive system a green coloration. However, the animals were not able to survive on this diet and it is questionable as to whether they were able to derive any nutrition from the algae.

The second time the life cycle was studied (1969-70), the hatched juveniles were immediately placed with the gymnoblast hydroid *Sarsia mirabilis* which was collected from the intertidal rocks at Nahant. Feeding began immediately and, in the continual presence of the food organism, individuals reached a length of 6.6 mm at 60 days post-hatch with the development of approximately 60 cerata on the dorsal surface (Fig. 2).

After ingestion there is an immediate coloration of the stomach as well as of the four extensions of the digestive gland in the four primary cerata. At this stage the left digestive gland supplies the anterior left and posterior pair of primary cerata. The smaller right digestive gland supplies the right anterior ceras. Externally the cerata appear bulky in feeding juveniles and at their tips the cnidosacs differentiate as internal opaque white structures. Squash preparations of living animals show an abundance of unexploded nematocysts stored in the cnidosacs. An animal that is disturbed with a probe under a dissecting microscope is seen to emit these unexploded nematocysts from the tip of the cerata. It would appear from the number of nematocysts present at any one time that they must be continually given off from the cerata in order to eliminate the structures from the digestive system. Food within the digestive gland extensions is continually flowing to and from the stomach by contractions of the cerata and ciliary action of the cells lining the gut. Very soon after feeding begins fecal pellets accumulate. The food-organism was orangish-pink but the fecal pellets were red. The nudibranchs graze on the entire hydroid colony but appear to prefer the undifferentiated tips of growing coenosarc.

The radula is used to graze on the hydroid and can be seen in a rasping motion during the feeding process. Squash preparations and whole mounts utilizing Turttox CMCS mounting media have shown that the newly hatched juveniles already have a radula with three to five rachidian teeth with well-developed denticles (Fig. 3). The radular teeth continue to increase in numbers during growth and in 10-40 day post-hatch juveniles there are from 8-12 rachidian teeth on the radular ribbon (Fig. 4). Toward the posterior portion of the radular ribbon (at about rachidian tooth 7) a pair of slender lateral teeth can be seen on the radular ribbon.

Juveniles that actively feed on the gymnoblasts begin to show formation of new cerata after about ten days of feeding. The first pair of new cerata form in front of the anterior pair of primary cerata (Fig. 9). The second pair arise in front of the second pair of primary cerata and the third single ceras differen-

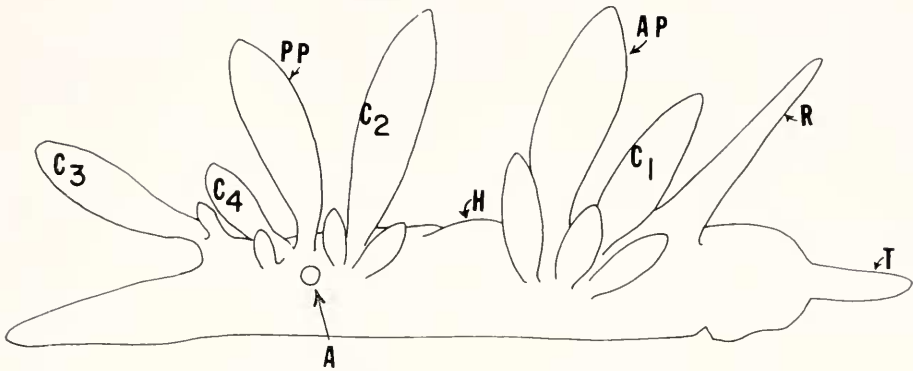


FIGURE 10. Diagrammatic representation of the sequential development of the cerata from the primary cerata (AP, anterior primary ceras; PP, posterior primary ceras). C_1 , C_2 and C_4 represent the right cerata of pairs while C_3 is a single posterior ceras. Other structures shown include the oral tentacle (T), anal opening (A), heart bulge (H) and rhinophore (R).

tiates at the posterior extremity of the nudibranch body (Fig. 10). The foot extends beyond this portion of the body. The cnidosacs of these new cerata differentiate several days after the initial cerata formation. The fourth pair of cerata develop just behind the second pair of primary cerata. Cerata formation continues in pairs with a second lower group being established on either side of the middle two rows. At this stage the nudibranchs measure 2.0–4.5 mm in length. The eyes gradually sink to a position on either side of the cerebral ganglion and are relatively small at this later stage in comparison to earlier post-hatch stages. The cerata are not as bulky in the 4.5 mm length nudibranchs and the whole animal takes on a slender adult-like appearance. There are scattered spots of white epidermal pigmentation at the four-cerata stage and as the animal continues to differentiate they coalesce into rings around the cerata (Fig. 2). The adult heart is clearly visible and beating at a length of 4.6 mm (Fig. 11).

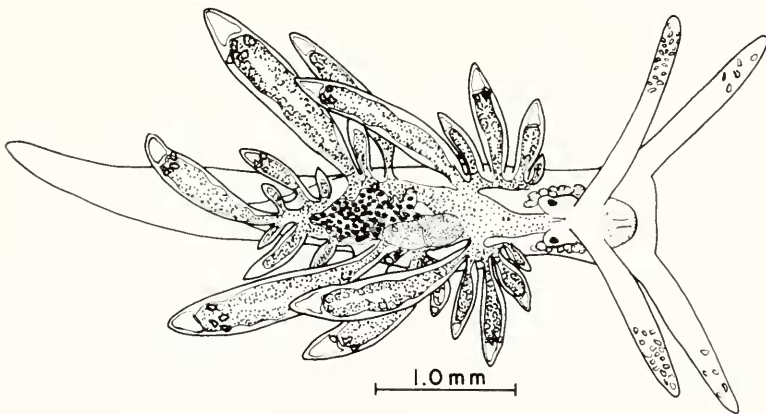


FIGURE 11. Juvenile *Coryphella stimpsoni* showing development of cerata at a length of 4.6 mm.

DISCUSSION

Verrill (1880) indicated that *Coryphella stimpsoni* bore a close resemblance to *Coryphella salmonacea* Couthouy. Both species have evenly spaced cerata as opposed to those species of *Coryphella* with cerata in distinct groups. In addition both species show a similar type of development in that the young crawl directly from the egg mass when hatching (Morse 1969a, 1969b). The differences between adults of the two species are that *C. stimpsoni* has a distinct trefoil surrounding the mouth, deposits egg strings in December, usually occurs on mudflats and will feed on burrowing sea anemones, while *Coryphella salmonacea* is generally larger, has only lateral bulges surrounding the circular mouth, deposits egg masses in March and April, and has only been found on rocky shores.

The radula of *C. stimpsoni* is variable within one animal as well as among several nudibranchs. Variations include the dentition of the central and lateral teeth, shape of the lateral teeth and numbers of rows of teeth in the adults. This is in contrast to Odhner's (1939) opinion that in the genus *Coryphella*, the radula is relatively constant in each species. Schönenberger (1969) described the variation of the radula of *Trinchesia granosa* Schmekel throughout its life-history. A comparable variation was seen in *C. stimpsoni* and points out the need for further studies on large numbers of nudibranchs of a species to determine if variability exists.

The development pattern of *Coryphella stimpsoni* is similar to development type 3 as described by Thompson (1967); that is the animal begins benthic life immediately after breaking out of the egg membrane. Two reports of development type 3 in eolid molluscs were listed by Thompson (1967), i.e., the report of Tardy (1962) on *Eolidina alderi* and that of Roginskaya (1962a) on *Cuthona pustulata*. In a second paper, Roginskaya (1962b) reported the development of *C. pustulata* in more detail. Schönenberger (1969) reported a similar development in *Trinchesia granosa*. The term direct development implies a juvenile crawling from the egg mass to a benthic existence, however *E. alderi* crawls out with the veliger shell still attached and *C. pustulata* loses the veliger shell after breaking out of the capsule but while still in the stroma of the egg mass. Both *T. granosa* and *C. stimpsoni* crawl out of the egg mass as juveniles with no shell.

Rao (1961) described the differentiation of the eolid *Cuthona adyarensis* which assumed a benthic existence after a short free-swimming veliger phase. Rao (1961), Roginskaya (1962b) and Schönenberger (1969) all reported in detail the development of the oral tentacles, the rhinophores and the sequence of differentiation of the cerata. It appears that these processes are very similar although there is a noticeable difference in the sequence of cerata differentiation which may prove to be species specific. In *Coryphella stimpsoni* the oral tentacle rudiments, rhinophore rudiments and the large dorsal visceral mass are already present when the nudibranch breaks through the membrane. The visceral mass soon equally forms four pruinordia of the primary cerata. The yolk present in the juvenile is enough to nourish the juveniles during the period of differentiation, although without the natural food further development is halted.

Thompson (1967) noted that four species of nudibranchs reported to have development type 3 have a boreo-arctic distribution which is also true of *Coryphella stimpsoni*. One of the four species mentioned by Thompson, *Cadlina lacvis*,

has been collected by the author within two miles of the locality from which the *Coryphella stimpsoni* were taken. *C. stimpsoni* is similar to *Cadlina laevis* in that the veligers and hatching juveniles are filled with yolk granules. In both species the embryonic period is long, there is a reduction of the velum and shell, and there is an absence of an operculum.

The term direct development is a bit misleading in the literature because of prior use, especially in relation to insect development. In the latter it generally refers to a series of embryonic stages where the animal's form closely resembles the adult. The juveniles do not have a distinct set of "larval characteristics." Among the molluscs the term has only been used for nudibranchs although many prosobranchs and pulmonates show a similar pattern of development. The important factors remain that there are a group of opisthobranchs which crawl directly from the enveloping capsule without a free-swimming veliger stage and in most cases when crawling-out show no external evidence of typical opisthobranch veliger morphology. Thompson (1967) has listed the characteristic reduction of veliger structures during early development which holds true of *C. stimpsoni* and which appears common to this form of development. It is suggested that his classification, i.e.,—"Development Type 3" be utilized in place of the often misleading term "direct development."

SUMMARY

1. The morphology and life history of the nudibranch mollusc, *Coryphella stimpsoni* (Verrill 1879) is described.
2. Adults were collected in October and deposited egg strings in December.
3. Development corresponds to Thompson's (1967) Type 3, i.e., juveniles crawl directly from the egg mass and begin benthic life.
4. Development time from egg deposition to the benthic crawling stage was from 25 to 52 days.
5. Veligers are characterized by a large amount of yolk, a reduced velum, a thin shell and no operculum.
6. Sequential development of tentacles, rhinophores and cerata and the differentiation of other organs such as cnidosacs, heart and digestive structures in the juveniles are described.
7. This is the first report of an eolid nudibranch from New England which crawls directly from the egg mass as a juvenile to begin benthic life.

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